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GENETIC STRUCTURE OF *NOTHOLITHOCARPUS DENSIFLORUS* (FAGACEAE) FROM THE SPECIES TO THE LOCAL SCALE: A REVIEW OF OUR KNOWLEDGE FOR CONSERVATION AND REPLANTING

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Abstract

Tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh (Fagaceae), is an important component of mixed-evergreen forests and woodlands in coastal California and Oregon, with incursions into the Sierra Nevada and the Klamath Ranges. Sudden Oak Death (SOD) is causing severe dieback and mortality in tanoak and could transform these ecosystems in areas where the pathogen *Phytophthora ramorum* S. Werres, A.W.A.M. de Cock can become established. Knowledge of genetic diversity within the species is important for both disease resistance screening, conservation and replanting in sites with high mortality. Here we review what has been learned about the genetic structure within tanoak since SOD has caused disease epidemics in the species. We review published work on genetic structure at the species level and provide some re-analyses of these data that show divergence across the geographic range. We also review recently published data on genetic structure at a fine spatial scale that provides some guidelines for the selection of trees as seed sources. Finally, we interpret a range of seed provenancing strategies in the light of our knowledge of tanoak genetic diversity.

Key Words: Conservation, fine-scale genetic structure, genetic divergence, *Notholithocarpus densiflorus*, replanting, tanoak.

Human-induced perturbations as a result of resource use, habitat fragmentation and climate change are leading ecosystems to functional tipping points with potentially far-reaching consequences (Barnosky et al. 2012). In forested ecosystems, the fine balance between a functioning system in which hosts and pathogens co-exist and the rapid decline that ensues when environmental conditions push the system out of equilibrium is an example of such a tipping point. Recently, this has been exacerbated by the movement of organisms globally, resulting in exotic diseases with catastrophic consequences. Forest trees are particularly vulnerable because of long generation times and sedentary life histories, but they are also critically important as keystone species of the broader ecosystem. Over the last century, several forest tree diseases have caused such severe host mortality that, what were once keystone species have been threatened or reduced from overstory trees to understory shrubs. Chestnut blight is a notable example on the American continent (Garnas et al. 2011) and pandemics of Dutch elm disease have been catastrophic across the northern hemisphere (Brasier and Buck 2002).

The current epidemic of Sudden Oak Death (SOD) caused by the exotic pathogen *Phytophthora ramorum* S. Werres, A.W.A.M. de Cock has a very wide host range and is shaping up to be a potentially devastating disease on tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh (Fagaceae), in central and northern California (Rizzo et al. 2005). Epidemiological risk analyses suggest that, like other systems, tanoak forests are likely to be transformed through the loss of overstory trees and may only avoid extinction through successful

resprouting (Cobb et al. 2012). If the disease takes the course predicted by Cobb et al. (2012), replanting will be necessary to augment genetic diversity that may be lost stochastically as stands regenerate vegetatively and to re-introduce diversity in stands that fail to resprout. Selection of suitable seed sources will be critical to the conservation of genetic resources as well as for successful replanting. There is considerable debate as to the optimum strategy for selecting seed sources that will maximize the likely success of local populations, while promoting a diverse gene pool on which selection can act if environmental conditions change (Breed et al. 2012). Seed collection from local sources to maximize likely locally-adapted genotypes may lead to inbreeding depression if population sizes have fallen below a threshold level (Eckert et al. 2010; Breed et al. 2012), whereas mixing seeds from different geographic sources introduces the risk of outbreeding depression if the source populations are from different locally adapted gene pools (Kramer and Havens 2009). Reciprocal transplant studies are helpful to gain some insights among these competing scenarios. However, for many tree species, such approaches are too time-consuming, so molecular marker data need to be used. Molecular methods allow the rapid documentation of genetic diversity, but in most cases sequences of DNA, or analyses of DNA fragment sizes are confined to regions of the genome that are not transcribed and are assumed to be selectively neutral. Although such DNA markers do not necessarily indicate genetic adaptations, they do provide us with information on evolutionary divergence that would indicate zones for conservation management (Moritz 1999) and seed sources that should not be mixed for planting if outbreeding depression is a concern.

Spatial organization of genetic diversity is a property of species that derives from contemporary demographic processes and past environmental events. At a broad spatial scale, encompassing a range of environmental conditions, evolutionary forces operate on the different gene pools and can lead to more or less divergent lineages (Hampe and Petit 2005). Detecting genetically divergent groups of individuals or populations is an area of interest in evolutionary biology (Pritchard et al. 2000; Manel et al. 2003; Waples and Gaggiotti 2006) and has consequences for the evolutionary trajectory of host responses to disease (Parker and Gilbert 2004) and for designing appropriate conservation programs (Grivet et al. 2008). At a local scale, genetic structure varies as a result primarily of the balance between dispersal and stochastic processes of chance representation of alleles (genetic drift). Knowledge of fine-scale genetic structure (FSGS) provides information on the spatial organization of pedigrees and the effective limits to recent seed and pollen dispersal. The latter can be important in resistance screening, where sampling of relatives may be desirable and in conservation and restoration where maximizing for genetic diversity in seed selection is the goal.

We have been studying genetic diversity in tanoak, with a view to understanding partitioning of genetic diversity at the broad (Nettel et al. 2009; Dodd et al. 2010) and fine-scale landscape levels (Dodd et al. 2013). Here, we review these earlier reports, re-analyze some of our earlier data with new tools and discuss the consequences for conservation and replanting strategies in the face of mortality from disease outbreaks. We refer to replanting rather than restoration because we are not proposing strategies to restore the ecosystem to its former state, but we are looking specifically at replanting of tanoak in areas where it has been lost through perturbations such as SOD.

The Species

Tanoak (*Notholithocarpus densiflorus*) was recently attributed to its monospecific genus by Manos et al. (2008) in recognition of its closer affinities to *Quercus*, *Castanea* and *Castanopsis* than to the Asian stone oaks (*Lithocarpus* spp.). Tanoak is a restricted endemic to the California Floristic Province; the tree form, *N. densiflorus* var. *densiflorus* ranges from disjunct stands in Ventura County, California to more continuous stands as far north as Coos County, Oregon (Tappeiner et al. 1990). Although it is best represented in the Coastal Ranges, it extends inland to the foothills of the Sierra Nevada. The dwarf form, *N. densiflorus* var. *echinoides* is more common at higher elevations in the north-eastern range of the species, particularly on serpentine. Occurrence reports of the dwarf form should be treated with caution as there is likely to be confusion over ecological dwarfism and genetically distinct forms (Dodd unpublished data). Tanoak is predominantly insect-pollinated (see Wright and Dodd this volume) and can produce heavy crops of acorns that have a relatively high viability; in addition it is a prolific basal sprouter.

Genetic Structure at the Species Level: Conservation Units

In defining management units for conservation under the pressures of climate change, Moritz (1999) argued for the greater importance of preserving distinct lineages over phenotypic or adaptive traits: while adaptations can be recreated given an adequate gene pool, historical processes cannot be repeated. Neutral genetic markers have been used extensively to detect lineages that have resulted from an overlay of

past events on biogeographic processes. Today, one of the greatest problems facing conservation geneticists is how to determine what constitutes distinct population lineages. In plants, chloroplast and nuclear genomes are the most commonly studied, but they may show distinctly different underlying patterns. Maternal inheritance of chloroplast DNA in most angiosperms commonly results in very strong geographic structure, particularly for heavy-seeded genera with short dispersal distances such as *Quercus* (Dodd et al. 2008; Grivet et al. 2008) and *Notholithocarpus* (Nettel et al. 2009). On the other hand, bi-parental inheritance of nuclear DNA results in much weaker geographic structure, as a result of large amounts of pollen with much greater dispersal distances than seed.

In tanoak, Nettel et al. (2009) detected four major and two rare chlorotypes based on four chloroplast microsatellite repeats (cpSSR) and one sequence region. No additional chlorotypes were detected in more extensive sampling of the species, particularly to the northern limit of its range in southern Oregon (Dodd et al. 2010). The four major chlorotypes included: 1. A coastal California type from Santa Barbara to Humboldt County, 2. A northern type from Humboldt County to the northern limit of the range in southern Oregon, 3. A Klamath Mountains chlorotype and, 4. A Sierra Nevada chlorotype (Fig. 1). Therefore, the chloroplast genome in tanoak displays a well-defined geographic structure, but low variation compared to California Floristic Province endemic oaks, such as coast live oak (*Quercus agrifolia* Née), for which we have detected 31 chlorotypes (Dodd et al. 2008) and valley oak (*Q. lobata* Née), for which 22 chlorotypes were detected Grivet et al. (2008). However, comparisons among species should be treated with caution because of potential variations in diversity at the selected gene loci. Although the geographic partitioning is informative on barriers to seed dispersal, it does not mean that seed dispersal can occur throughout the geographic range of a chlorotype. Analysis of more of the chloroplast genome could reveal further variation within any of the four major types detected. Perhaps the most interesting finding from these results is the marked break between the northern and southern coastal types near Arcata, CA (Humboldt County) and the divergence between coastal and interior populations of tanoak. The former split is of greatest interest for SOD outbreaks and suggests northern and southern coastal lineages that have been separated and only recently come into secondary contact. Whether the two lineages differ in their tolerance to *P. ramorum* remains to be seen, but preliminary data do suggest low, but significant variation among populations (not including the northern coastal chlorotype) in response to inoculation (Hayden et al. 2011).

Do Nuclear DNA Markers Support Divergence Revealed By The Chloroplast Genome?

As for other members of the Fagaceae (Sork et al. 2010), only weak genetic structure was detected among populations of tanoak (Nettel et al. 2009). This is generally interpreted to be a result of widespread pollen dispersal in many trees species (Ashley 2010). Field sampling for phylogeographic studies is commonly designed to cover the range of distribution of the species and to capture any potentially, naturally isolated groups of individuals. Unfortunately, although sampling locations are commonly referred to as populations, there is no a priori knowledge of what constitutes a genetic population, often interpreted as a panmictic group (but see Palsbøll et al. 2007), which then becomes a problem of post hoc inference. To infer panmictic groups, Nettel et al. (2009) used the Bayesian approach implemented in STRUCTURE (Pritchard et al. 2000). However, it is well accepted that when genetic structure is weak, the program STRUCTURE does not perform well in detecting the number of groups. An alternative Bayesian analysis BAPS performed on a larger data set, including more extensive sampling in southern Oregon, detected nine clusters (Dodd et al. 2010). However, although the BAPS assignments indicate spatially consistent grouping of populations, they do not show the relative importance of the partitions.

Here, we have extended our analyses using the software Barrier vs. 2.2 (Manni et al. 2004). The advantage of this analysis is that a hierarchy of importance of discontinuities and their direction on the landscape can be inferred. Barrier uses central coordinates for a sampled population first to calculate a Voronoi tessellation and then a Delaunay triangulation that draws a network connecting all the sample localities. The Monmonier's (1973) maximum-difference algorithm then takes a distance matrix (genetic distance) to identify boundaries, where differences between pairs of populations are greatest. The significance of these barriers can be tested by bootstrapping the distance matrix after re-sampling genotypes in each population. We used the population comparisons option in Arlequin 3.5.1.3 (Excoffier and Lisher 2010) to obtain a matrix of population pairwise genetic distances (Slatkin's linearized F_{ST}). To bootstrap distance matrices, we first re-sampled genotypes with replacement 100 times in each of the populations using the Excel add-in provided by Resampling Stats, Inc., Arlington, Virginia, USA. We then re-calculated the matrices of population pairwise Slatkin's linearized F_{ST} for each of the 100 re-sampled data sets. We ran Barrier to detect the locations of the first five

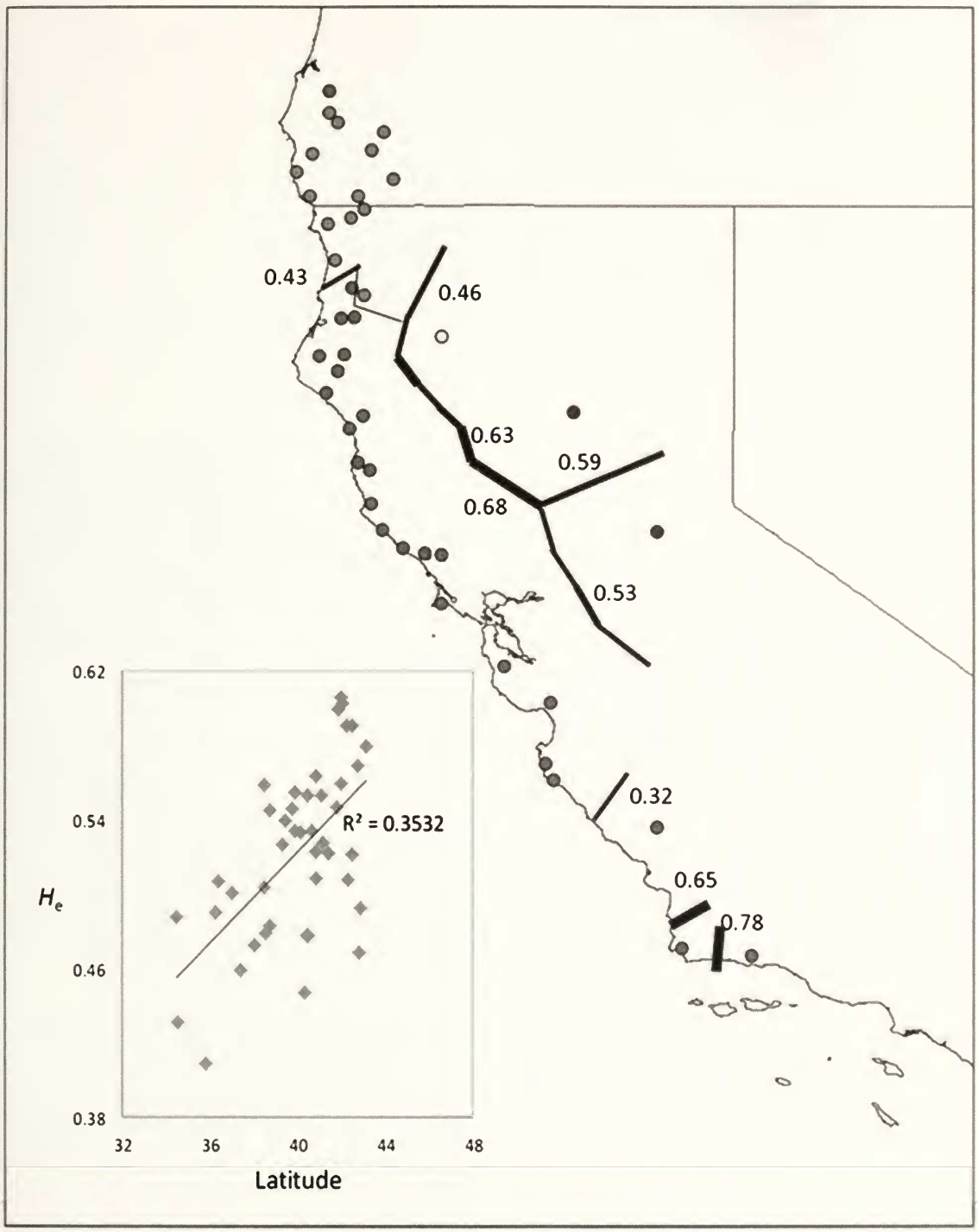

FIG. 1. Map of chloroplast and nuclear DNA breaks in the distribution of tanoak (*Notholithocarpus densiflorus*). Filled circles show sampling locations with colors depicting different chlorotypes (adapted from Dodd et al. 2010). Lines show the major breaks in nuclear DNA from BARRIER analysis of population pairwise Slatkin's linearized F_{ST} conducted in this report. Thickness of line segments are proportional to the ratio of F_{ST} of that segment to maximum F_{ST}. Numbers next to thickest line segments show proportional bootstrap support after resampling 100 times within populations. Inset shows relationship between expected heterozygosity (H_e) and latitude of origin of population (adapted from Nettel et al. 2009).

barriers in the genetic distance matrix and used the resampled data to determine bootstrap support.

The breaks detected by Barrier are shown in Figure 1 as lines of variable thickness corresponding to the ratio of the F_{ST} for each line segment divided by the maximum F_{ST} detected, as recommended by Manni et al. (2004). For clarity, bootstrap support values are shown only for the thicker line segments for each of the breaks. Interestingly, the first two barriers detected were in the southern range of tanoak between Santa Barbara and Lompoc and between Lompoc and Nacimiento respectively. Both of these breaks received strong bootstrap support. The third barrier separated interior populations from the Klamath Mountains and the Sierra Nevada from Butte County from coastal populations. The thickness of these segments tended to decrease northwards indicating a weaker divergence northwards, consistent with our earlier STRUCTURE analyses that grouped these populations with the northernmost coastal California group of populations and those from Oregon (Nettel et al. 2009). Interestingly, the Barrier analysis detected divergence between Sierra Nevada populations from Butte and El Dorado Counties. The fourth barrier continued the separation of interior and coastal populations southwards, with the greatest divergence between the El Dorado County population and those from the San Francisco Bay Area. The thickness of the segments decreased northwards as this barrier joined the third barrier and also decreased southwards. The fifth break that was detected separated north coastal and south coastal populations east of Arcata, California (Humboldt County). Notably, this barrier passed between two nearby populations from Korbel and Hoopa (Humboldt County), consistent with the partition between the northern and southern coastal chlorotypes shown in color in Figure 1.

These new analyses of nuclear DNA support the divergence between coastal and interior populations and between north and south coastal populations detected from chloroplast DNA. In addition, they reveal probable isolation and fragmentation in the southernmost range of the species that was not evident from the chloroplast data.

What Can We Infer From Divergence?

Following Moritz (1999), we are looking for divergent lineages that have arisen because of past events; the most important for many plant taxa were the glacial cycles that have occurred over the last approximately 2 million years and the more recent Holocene warming. The major divergences in population lineages in tanoak do suggest correlations with these past events. The southern range of tanoak has likely been most influenced by changes to a drier climate in the late Holocene (Kirby et al. 2007). Indeed, Nettel et al. (2009) inferred decreases in effective population size since the mid-Holocene. Today these populations are fragmented and relatively small and represent the trailing edge of the species. Genetic diversity, measured as expected heterozygosity, is least in these southern small and fragmented populations and increases northward (Fig. 1). Divergence across the Great Central Valley of California is not unexpected. Many taxa display deeper divergence between the Sierra Nevada and Coastal Mountain Ranges than within the mountain ranges, although this tends to be less clear for tree species (Calsbeek et al. 2003). However, it was surprising that a barrier was detected within the Sierra Nevada Range, between the Butte County and El Dorado County populations. More extensive sampling is needed to confirm this. Finally, the divergence between north coastal and south coastal populations shown most clearly with chloroplast DNA, and supported by nuclear DNA, shows a remarkable delineation over a very short distance. Indeed Dodd et al. (2010) reported only one population in which they found a mixture of the two chlorotypes. The most likely explanation is that climatic changes in the past resulted in restriction of tanoak north and south of this region that has only very recently become a zone of secondary contact. Taken together, the chloroplast and nuclear data suggest that the range of tanoak can be divided into at least four groups that should be considered in conservation efforts: 1. A northern group from Arcata to Oregon, 2. A northern and central California coastal group from Arcata south to Monterey County, 3. One or more interior groups (additional population sampling is required to determine the limits of these lineages) and 4. Two or more trailing edge populations in the southernmost range of the species.

Within Population Genetic Structure: Seed Sources for Replanting

Conventional thinking dictates that local seed sources for replanting should provide gene pools that are well-adapted to the local environment (Broadhurst et al. 2008; Kramer and Havens 2009). However, severe mortality from disease may lead to drastic reductions in effective population sizes, with consequent risks of inbreeding (including mating among close relatives). In outbreeding species that typically have high genetic load, inbreeding depression is likely to be expressed. The risks of inbreeding depression are even greater in species that spread through vegetative reproduction because of the increased pollen supply from spatially clustered genetically identical ramets.

Tanoaks can produce large acorn crops and also reproduce prolifically by basal resprouts. The large heavy seeds are dispersed by gravity, or by birds and small mammals, so that seed dispersal distances are likely to be short (Scofield et al. 2010; Moran and Clark 2012). This, combined with the potential local accumulation of stems of resprout origin should result in fine-scale genetic structure composed of demes of related individuals. The spatial scale of clonality and of relatedness become important parameters in determining the minimum distances that should be observed in selecting trees for seed collection to minimize risks of increased inbreeding in re-vegetated sites.

Clonal Spread

Detection of members of a clone (ramets) requires molecular markers with sufficient power that a pair of individuals with identical genotypes can be confidently assigned to a clone and are unlikely to be of seed origin. Using a set of eight nuclear microsatellite markers, Dodd et al. (2013) reported an average of 1.6 ramets per tanoak genet in mature upland and lowland stands. A frequency histogram of numbers of ramets per genet shows large numbers of single-ramet genets and a maximum of five ramets per genet on lowland sites and eight ramets per genet on upland sites (Fig. 2a). The maximum spatial distance over which the ramets were distributed, estimated as the zero intercept of a logistic function fitted to a plot of frequency distributions of different distance classes (Fig. 2b) was 6.5 m on upland sites and 5.5 m on lowland sites. One problem with rapidly mutating markers such as nuclear microsatellites is ramets may not have identical genotypes because of somatic mutations (Ally et al. 2008). Therefore, if resprouting has been occurring over generations, different mutations could arise among the ramets and the estimates of ramet number and distance based on identical genotypes could be underestimated. Although Dodd et al. (2013) allowed for a single step mutation at their microsatellite loci for assignment of non-identical ramets to a genet lineage (multilocus lineages), this did not increase significantly the estimates of numbers and spread of ramets. Based on the single location for their study, clonal spread appears not to have exceeded about 6–7 m.

Spatial Genetic Structure

Fine-scale genetic structure for neutral genetic markers arises mainly as a result of the balance between gene dispersal and stochastic processes of genetic drift. Assuming a population to be in drift-dispersal equilibrium, genetic neighborhoods that define a circle within which parents

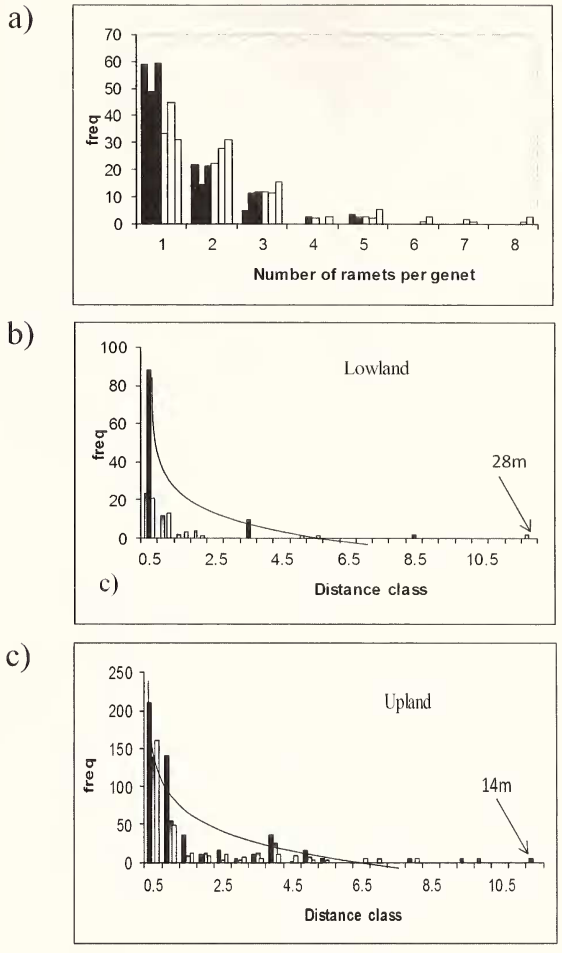

FIG. 2. (a) Frequency distribution of numbers of ramets per genet (solid bars: lowland sites and unfilled bars: upland sites); (b and c) frequency distributions for clone mates within distance classes for lowland and upland sites (three replicate sites shown as grey, solid and open bars. Fitted logarithmic function $y = -13.8 \ln(x) + 22.8$ for lowland site and $y = -39.9 \ln(x) + 74.5$ for upland site. Adapted from Dodd et al. (2013).

of most of the individuals reside, can be estimated using classical population genetic theory for models of continuous populations (Wright 1943). A two-dimensional neighborhood size ($Nb = 4\pi\sigma^2 d$) is normally distributed with radius 2σ, where σ (standard deviation of dispersal) defines the displacement of progeny from parents, and d is the population density. Neighborhood size (Nb) can be inferred from spatial patterns of relatedness estimated from molecular data that allows inference of σ^2 (Vekemans and Hardy 2004) and effective plant density. Wright's model can be extended to include the composite effects of seed dispersal, pollen dispersal and vegetative spread (Gliddon et al. 1987). Dodd et al. (2013) estimated neighborhood sizes in tanoak as a function of clonal spread and of sexual dispersion. Clonal

spread averaged 1.7 m on lowland sites and 2.1 m on upland sites, whereas sexual dispersion averaged 69.3 m on lowland sites and 46 m on upland sites. These dispersal distances are evolutionary measures that make a number of assumptions, most importantly that populations are in equilibrium and that dispersal follows a normal distribution. Neither of these assumptions is realistic; populations need long periods of environmental stasis to reach equilibrium and dispersal distances are more likely to be leptokurtic with most progeny being close to parental individuals. Nevertheless, the estimates of dispersal distances from genetic neighborhoods provide the best indications of how far apart trees for seed collection should be to minimize relatedness, in the absence of direct estimates from progeny arrays (multiple seeds from a single parent) to infer parentage.

Implications for Replanting

Present indications are that the SOD pathogen will continue to cause epidemics resulting in severe mortality of tanoak trees and that the ecosystems in which tanoak is dominant are likely to be transformed, with tanoak being represented only in the understory as resprouts (Cobb et al. 2012). So far, ecological monitoring is insufficient to determine the long-term survival of resprouts, or whether some genotypes are likely to be more persistent than others as clones. Assuming continued mortality of adult trees, stands through which disease has spread will have smaller effective population sizes, as fewer individuals will reach seed-producing age. To augment the loss of tanoak, vegetation managers need guidelines for the selection of seed for replanting. Breed et al. (2011) describe a range of seed sourcing strategies aimed at minimizing the effects of inbreeding and outbreeding depression, avoiding or mitigating introduction of mal-adapted genotypes and providing a diverse genetic base for adaptation to environmental change. We examine these options for tanoak and recommend under what circumstances they may be appropriate and what further research is needed to optimize success of replanting.

Local Provenancing

Although the use of local seed sources is the most commonly adopted strategy, it is best reserved for a system in which only local populations exist (Breed et al. 2012). Under these conditions risks of outbreeding depression and introducing mal-adapted genotypes are minimized. For tanoak this may be important in peripheral populations such as the southern range where populations are more isolated (see discussion above) and in the interior coastal range where populations reach their distributional limit. There are two major disadvantages of this approach. First, if populations are small, they may not be optimally adapted to their local environment because of genetic drift. This will be exacerbated by the selection of a relatively small seed pool for replanting. If adopted, seed should be selected from trees that are least likely to be related. Ideally, research is needed to determine dispersal distances of seed and pollen to determine minimum distances among seed trees for each population in need of replanting. If this is not possible, the minimum distances described above from the study at Jackson Demonstration State Forest can be applied. However, we know very little about pollen dispersal in this insect-pollinated species and factors affecting pollinators will play an important role in the size of genetic neighborhoods. The second disadvantage of local provenancing is that it does not account for environmental change. This is likely to be very important in the southern range of the species, including areas of high mortality levels in Monterey County.

Predictive Provenancing

This approach requires information on plant performance under a range of experimental conditions. This can be provided by reciprocal transplant studies, but these have not been performed for tanoak. The great advantage of this technique is that phenotypes can be identified that should perform well at the replanting site. Furthermore, climate modeling can provide some inferences on future climate at the site so that phenotypes can be selected that are expected to match future climates. Substantial work is needed before this approach can be implemented for tanoak. However, reciprocal transplant plots are a worthy investment to obtain valuable information on translocation success.

Composite Provenancing

The objective of this approach is to attempt to mimic landscape patterns of gene flow and to incorporate a mix of planting stock that reflects the probable pool of genotypes that would naturally contribute to the evolutionary potential of the site (Broadhurst et al. 2008). This requires knowledge of patterns of gene flow and differentiation at scales from 100s to 1000s of meters. This scale is intermediate between the species-scale and the fine-scale described above for tanoak. Advantages of this approach are that seed provenances can be detected that are tied together by gene flow and quantities of seed from the different sources can be selected so that the risk of genetic swamping and introduction of mal-adapted genotypes is low, and provenances can be selected that account for climate change.

Genetic data at this scale are not available for tanoak, but they could be obtained at relatively low cost.

Admixture Provenancing

Admixture provenancing (Breed et al. 2012) selects seed from different environmental conditions within large populations. Unlike composite provenancing, no account is taken of dispersal distances, but sampling can be skewed to favor seeds from sites whose climate is likely to match future climate at the replanting site. Although, this approach is likely to introduce maladapted genotypes, Breed et al. (2012) claim that these should rapidly be purged from the population, but this would require large numbers of seedlings and would introduce the risk of outbreeding depression in the next generation. Therefore, provenances taken at great distances from the replanting site should first be tested in crossing studies and reciprocal transplants. For tanoak, we highly recommend that this type of approach should not mix provenances from the five major groups (Santa Barbara, Lompoc, central and northern coastal California, extreme northern California and Oregon, interior populations from the Sierra Nevada) described under Genetic structure at the species level above.

Conclusions

Our knowledge of genetics of tanoak is still at an early stage, but it does provide some guidelines that will be important for future management of tanoak stands if SOD continues to cause high levels of mortality. Here we have reviewed some of the published work that addresses population processes and the implications for choice of seed sources for replanting after mortality from SOD. In this issue, Wright and Dodd provide evidence that tanoak is insect pollinated that contrasts with the pollination syndrome in the true oaks. This is likely to have implications for patterns of pollen dispersal that in turn will be influenced by environmental changes associated with the disease, with population fragmentation and with climate change. We still have much to learn about the ecological processes that affect genetic diversity in this species and the consequences for conservation and revegetation under the combined challenges of disease, development and climate change.

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